

Occurrence: Forbes Formation of the Chico "series" (KIRBY, 1943) in the Rumsey Hills, Yolo County, California; from Campanian strata (see Appendix for locality descriptions).

DISCUSSION

The distribution of *Tibiaporrhais* in the North Pacific, Western Interior, and Gulf Coast regions of North America further supports SOHL's (1967, 1971) suggested link between the North Pacific and Western Interior regions during the Late Cretaceous. Based on similarities in the distribution patterns of gastropod genera, particularly between Sakhalin and the Western Interior region (SOHL, 1967), SOHL (1971) hypothesized a northern migration route between the regions or an unknown "boreal" fauna supplying migrants to both regions simultaneously.

In addition, morphological similarities between the shells of *Tibiaporrhais* and the Indo-Pacific genus *Tibia* suggest a possible evolutionary link between these genera; both share the general characteristics of having (1) a high spire, (2) broadly convex whorls, (3) weak sculpture consisting primarily of fine spiral striae and axial growth lines, (4) a moderately flaring lip with digitations, and (5) a long to moderately long anterior siphonal canal that is straight to slightly bent (compare Figures 1 and 5). One notable difference in shell morphology between *Tibiaporrhais* and *Tibia* is the development of the posterior canal and callus on the spire of the latter genus. *Tibiaporrhais* is here placed in the Aporrhaidae based on the aporrhaid characteristics of (1) a high-spined shell having many whorls, (2) the two spinelike processes extending from the outer lip, and (3) the slightly bent, spinelike anterior canal. *Tibia* is presently assigned to the Strombidae, but differs from most strombids in having a higher spire, longer anterior canal, and lacking the "stromboid notch" that allows protrusion of the stalked right eye (ABBOTT, 1960); however, *Tibia* does possess the strombid features of stalked eyes, a hooklike operculum, and a long foot (H. & A. ADAMS, 1853; ABREA, 1975).

With POPENOE's (1983) reassignment of the genus *Pugnellus* Conrad, 1860, from the Strombidae to the Aporrhaidae, the earliest undoubted strombid is of latest Maastichtian age (POPENOE, 1983). Thus, *Tibia* possibly belongs to a conservative ancestral stock of strombids descending from or of common ancestry with *Tibiaporrhais*, and which split from the main stock of Strombidae at an early point in its radiation. *Tibia* may therefore retain some aporrhaid features while possessing some strombid characters. The ambiguous nature of *Tibia* and its similarity in shell morphology to *Tibiaporrhais* indicate the need for a comparative analysis of the soft-part anatomy of extant *Tibia* and other Strombidae and Aporrhaidae in order to assess properly their evolutionary relationships. Comparative analysis of DNA sequencing in these groups may also shed light on this problem. The results of such studies should determine the family to which *Tibia* is more closely allied, and whether the similarities in shell morphology between *Tibia*

and *Tibiaporrhais* reflect a close evolutionary relationship or merely homeomorphy in genera from two families of Strombacea.

ACKNOWLEDGMENTS

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APPENDIX

Locality Information

- USGS Collection 14063. Branch east of Texas Midland Rail Road, 0.4 mi. (0.6 km) N of Cooper, Delta County, Texas. Greenish-gray calcareous clay (marl) with calcium carbonate concretions. Collected by L. W. Stephenson, 1928.
- UCM Locality 81007. Near top of S side of prominent SE pointing butte. Grand County, Colorado, Kremmling 1:62,500 Quadrangle, NW $\frac{1}{4}$ SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 7, T3N, R80W. Collected by J. Kirkland, 1981-1982.
- USGS Mesozoic Locality M4013. SE side of intermittent creek, S of Petroleum Creek, N of Guinda VABM, Yolo County, California. Rumsey 1:24,000 Quadrangle, 1450 ft. (442 m) E and 2450 ft. (747 m) S of NW corner of sec. 11, T12N, R3W. Collected by E. Pessagno, 1965-1966.

Relocation of *Ervilia* Turton, 1822 (Bivalvia) from the Mesodesmatidae (Mesodesmatoidea) to the Semelidae (Tellinoidea)

by

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Abstract. *Ervilia* Turton, 1822, is represented by a few small tropical and subtropical species. The familial placement of the genus has been in question since its original description. On the basis of hinge and ligament structure, the presence of a posteroventral cruciform muscle in the fused ventral mantle margins, and other anatomical features, *Ervilia* is here relocated from the Mesodesmatidae (Mesodesmatoidea) to the Semelidae (Tellinoidea). We suggest that the *Erviliinae* Dall, 1895, be abandoned and that the remaining constituent genera, i.e., *Coecella* Gray, 1853, and *Argyrodonax* Dall, 1911, be temporarily relocated in the Mesodesmatinae pending fuller revision of the Mesodesmatidae and Mesodesmatoidea. Lectotypes are designated for *Ervilia nitens* (Montagu, 1808) and *Ervilia castanea* (Montagu, 1803).

INTRODUCTION

According to contemporary authorities (BEU, 1971; SAKURAI & HABE, 1973; VOKES, 1980; BOSS, 1982), the Mesodesmatidae Gray, 1840, comprises three subfamilies: Mesodesmatinae Gray, 1840, Daviliinae Dall, 1895, and *Erviliinae* Dall, 1895. Several representatives of the Mesodesmatinae have received extensive study, e.g., *Mesodesma arctatum* (Conrad, 1830) (ALLEN, 1975) and *M. mactroides* Deshayes, 1854 (NARCHI, 1981). NARCHI (1980) reported on the functional morphology of *Caecella chinensis* Deshayes, 1855 (*Erviliinae*). YONGE & ALLEN (1985) investigated *M. arctatum*, *Atactodea striata* (Gmelin, 1791) (Mesodesmatinae), *Davila plana* (Hanley, 1843) (Daviliinae), and *Ervilia castanea* (*Erviliinae*) and concluded that they were all similar to each other in terms of ligament structure and collectively different from the Mactridae, such that the Mesodesmatidae Gray, 1840, should be separated from the mactrids and placed in their own superfamily, the Mesodesmatoidea Gray, 1840.

MORTON (in press) and this paper demonstrate significant anatomical differences in *Ervilia castanea* from the mesodesmatoid plan, unnoticed by YONGE & ALLEN (1985). This paper investigates the type material of *Ervilia nitens*, the type species of *Ervilia*, and *E. castanea* and summarizes significant anatomical features of the latter that justify separation of the genus from the Mesodesmatidae. It also examines likely relatives of *Ervilia* and recommends placement in the Semelidae Stoliczka, 1870 (Tellinoidea).

SYSTEMATIC TREATMENT

Designation of Lectotypes

In the recent systematic treatments of *Ervilia* (ROOIJ-SCHULING, 1972, 1973; DAVIS, 1973; BABIO & BONNIN, 1987) lectotypes were not selected for Montagu's two species of *Ervilia*. To stabilize the taxa treated in this paper, we have selected lectotypes for *Ervilia nitens* and *Ervilia castanea*.

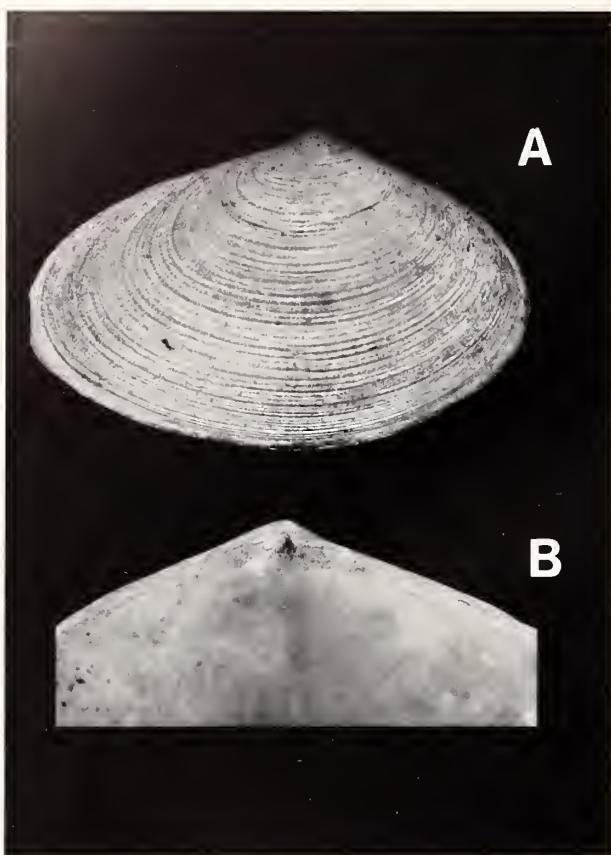


Figure 1

Ervilia nitens (Montagu, 1808); **Lectotype (herein)** of *Mya nitens* Montagu, 1808; right valve, Dunbar, Scotland; Royal Scottish Museum 1866.21a.43. A. Exterior, 7.0 mm length, 4.4 mm height. B. Close-up of hinge.

Ervilia nitens (Montagu, 1808)

(Figure 1)

Mya nitens MONTAGU, 1808:165–166. [Type species (monotypy) of *Ervilia* TURTON, 1822:56, pl. 19, fig. 4.]

DALL (1896), ROOIJ-SCHUILING (1972, 1973), and DAVIS (1973) present synonymies, a diagnosis, and distributional information for this species.

The type of *Mya nitens* was first described from specimens found in Dunbar, Scotland. FORBES & HANLEY (1853), however, believed such shells to have been brought to Europe in ballast sand from the Caribbean. This hypothesis was accepted by ROOIJ-SCHUILING (1973) and DAVIS (1973) as the only plausible explanation for the lack of new records for this species in the northeast Atlantic Ocean. *Ervilia castanea* is the only species of the genus that occurs in British waters (ROOIJ-SCHUILING, 1973; BABIO & BONNIN, 1987).

We have selected syntypes from the Royal Scottish Museum (RSM) that were previously in the collection of

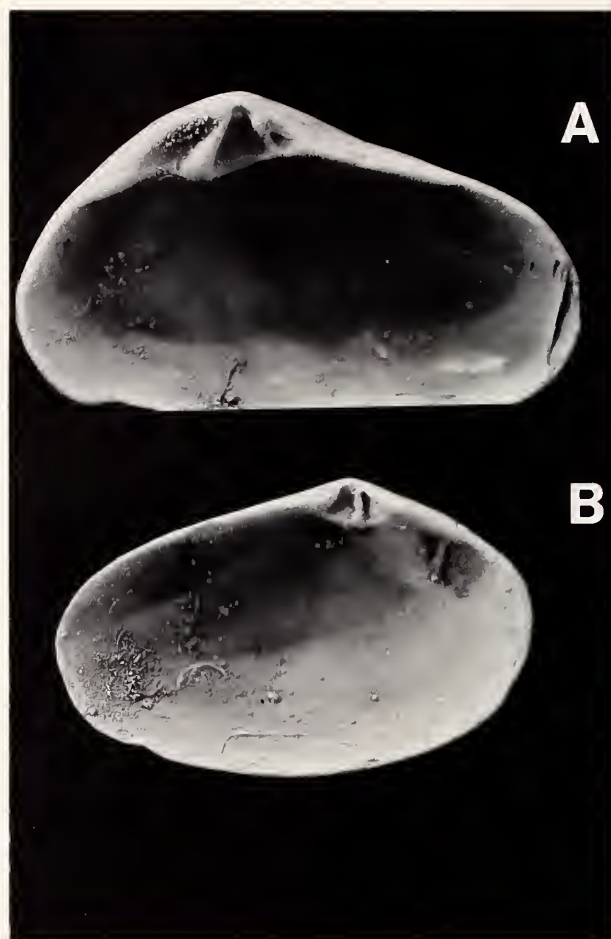


Figure 2

Ervilia castanea (Montagu, 1803). A. **Lectotype (herein)** of *Donax castanea* Montagu, 1803; internal of right valve, 10.4 mm length, 6.5 mm height; Devon, England; Royal Albert Memorial Museum, Exeter 3729. B. Paralectotype; internal of left valve, 8.8 mm length, 5.5 mm height; same locality and catalogue number as lectotype.

William Bean, a contemporary of Montagu (DEAN, 1936). We cannot prove this material was studied by Montagu, but owing to the very few specimens collected in the region and the association with Bean and Montagu, it does seem highly probable that this was the case. These RSM syntypes were reported by ROOIJ-SCHUILING (1972) as "possible paratypes." Syntypic specimens were not located in the British Museum (Natural History) (S. Morris, personal communication, January 1988) or the Royal Albert Memorial Museum, Exeter (J. D. Taylor, personal communication, July 1989).

Lectotype (herein): RSM 1866.21a.43; right valve; length = 7.0 mm, height = 4.4 mm (Figure 1A, B). Paralectotypes (additional specimens from lectotype lot, RSM 1866.21a.43); 1 intact pair and 2 left valves. Type locality:

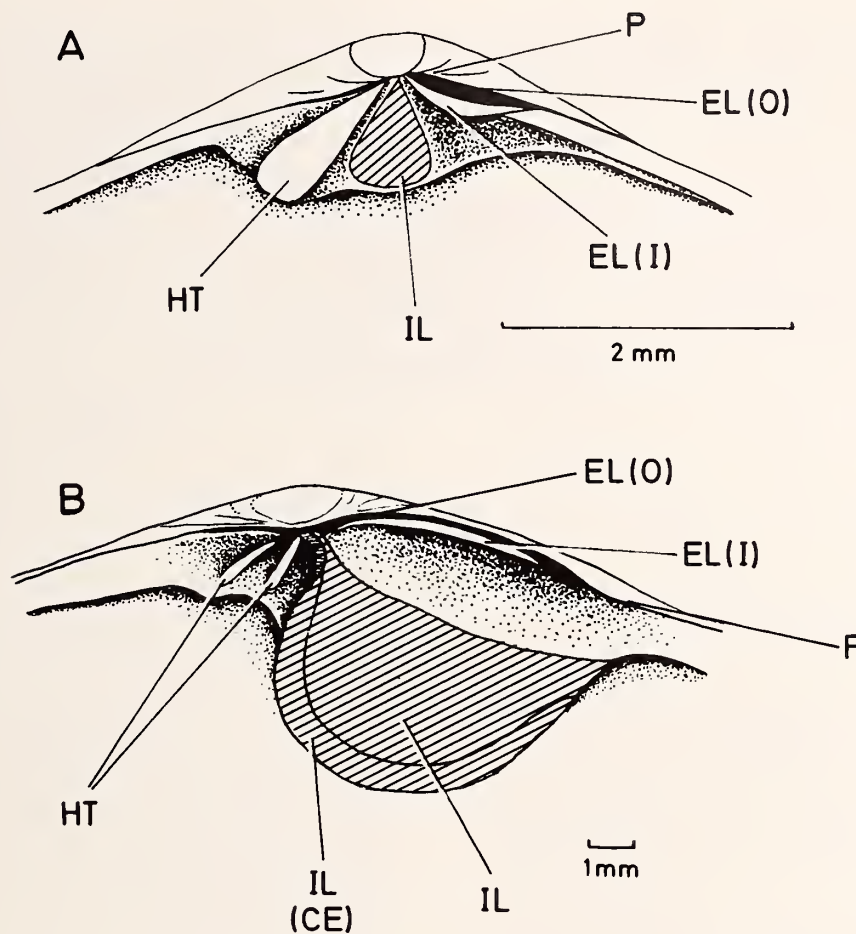


Figure 3

Detail of hinge plates of the right valve. A. *Ervilia castanea* (Montagu, 1803) (after MORTON, in press). B. *Scrobicularia plana* (da Costa) (after TRUEMAN, 1953). Key: EL(I), inner element of external ligament; EL(O), outer element of external ligament; HT, hinge tooth; IL, inner ligament; IL(CE), cut edge of inner ligament; P, periostracum.

SCOTLAND, Lothian region, Dunbar; ca. 56°00'N, 02°30'W. The distribution of *Ervilia nitens* appears to encompass the western Atlantic Ocean and the Caribbean Sea (ROOIJ-SCHUILING, 1973; DAVIS, 1973).

Ervilia castanea (Montagu, 1803)

(Figures 2, 3A, 4)

Donax castanea MONTAGU, 1803:573, pl. 17, fig. 2.

Diagnoses and distributional information for *Ervilia castanea* are provided in TEBBLE (1966), ROOIJ-SCHUILING (1973), BABIO & BONNIN (1987), and MORTON (in press).

As with *Ervilia nitens*, and in spite of several taxonomic treatments of this species, a lectotype has never been selected. Syntypes from the Montagu collection were found in the Royal Albert Memorial Museum, Exeter (RAME) glued to their original card (catalogue No. 3729) (see DEAN, 1936).

Lectotype (herein): RAME 3729; right valve; length = 10.4 mm, height = 6.5 mm (Figure 2A). Paralectotype (attached to same card as lectotype); left valve; length = 8.8 mm, height = 5.5 mm (Figure 2B). Type locality: ENGLAND, Devon; ca. 50.2°N, 04.0°W.

Anatomical Features of *Ervilia castanea*

MORTON (in press) identified two important anatomical features that clearly separate *Ervilia* from the Mesodesmatidae, i.e., the ligament and a cruciform muscle. Other details of the general morphology support this distinction.

The ligament and hinge plate: Hinge narrow to robust; left valve with two small anterior teeth separated by a deep socket (Figure 2B); right valve with large anterior tooth that interlocks into socket of left valve (Figures 2A, 3A); resilifer directly below beaks; small tubercle posterior of resilifer in both valves; obscure lateral teeth present in both valves.

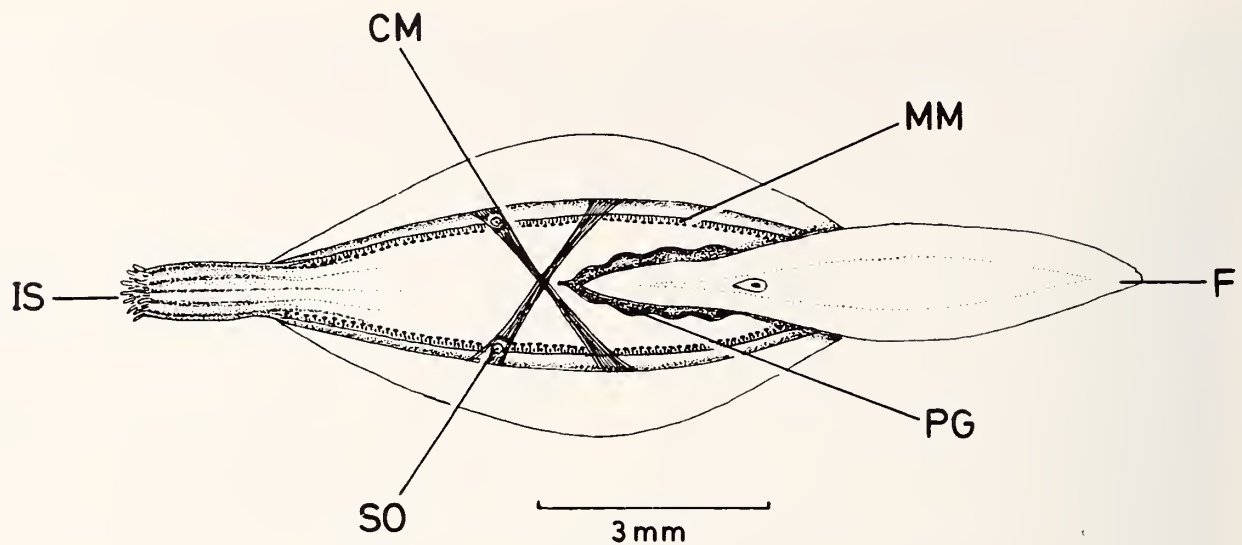


Figure 4

Ervilia castanea (Montagu, 1803). Ventral view showing cruciform muscle. Key: CM, cruciform muscle; F, foot; IS, inhalant siphon; MM, mantle margin; PG, pedal gape; SO, sense organ (after MORTON, in press).

The ligament (Figure 3A) is complex and comprises a posteriorly directed (opisthodetic) external element (EL) and an amphidetic internal element (IL). The external element comprises an outer layer [EL(O)] and an inner layer [EL(I)] and is overlain by thin periostracum (P).

The cruciform muscle: Posteroventrally, in the region of the left and right mantle fusion between the inhalant siphon and pedal gape, the left and right shell valves are united by a cruciform muscle (Figure 4, CM). It comprises two compact bundles of muscles extending diagonally between the shell valves and crossing over at the midline of pallial fusion. Close to the shell, the posterior ends of the bundles each possess a sense organ (SO). The cruciform muscle of *Ervilia castanea* has been described by MORTON (in press) who also describes the sense organ and shows that it is "open" like that of *Scrobicularia*, as opposed to "closed" as is the case in *Donax*, *Tagelus*, and *Sanguinolaria* (FRENKIEL, 1979; FRENKIEL & MOUEZA, 1984).

Other features: The siphons are long and separate and formed by fusion of the inner mantle folds only (Type A) (YONGE, 1957, 1982). The ctenidia are large, homorhabdic, eulamellibranch, and non-plicate and the ciliary currents are of Type C(1) (ATKINS, 1937). The labial palps are small and the ctenidial-labial junction is of Category 3 (STASEK, 1963). The stomach is of Type V (PURCHON, 1987) but much simplified in this small species (MORTON, in press).

Alcohol preserved specimens of this species collected in the Azores are vouchered in the Santa Barbara Museum of Natural History (SBMNH 35147).

DISCUSSION

MONTAGU (1803) first described *Donax castanea* and later *Mya nitens* (MONTAGU, 1808). The latter is the type species (monotypy) of *Ervilia* Turton, 1822, which was placed in the Donacidae by FORBES & HANLEY (1853), and in the Paphiidae by SMITH (1885). DALL (1895) relocated *Ervilia* in the Mesodesmatidae and erected a new subfamily Erviliinae, which also included *Coecella* Gray, 1853, formerly placed in the Mactridae. LAMY (1914) agreed that both genera were members of the Mesodesmatidae but made no mention of the Erviliinae. Placement of *Ervilia* and *Coecella* in the Mesodesmatidae by both authors was on the basis of shell features, although DALL (1898) admitted the "nomenclature of the genera comprised in this family has always been more or less confused."

DALL (1911) erected the genus *Argyrodonax* in the Erviliinae based on a single specimen of *A. haycocki* from Bermuda. DALL (1924) also erected *Rocheffortina* as a subgenus of *Rocheffortia* (Montacutidae) but DALL *et al.* (1938) subsequently elevated *Rocheffortina* to generic rank and placed it in the Erviliinae. IREDALE (1930) introduced the new genus *Spondervilia* without a description but named *Ervilia australis* Angas, 1877, as the type species. DALL *et al.* (1938) placed *Spondervilia* as a subgenus of *Ervilia* and differentiated the former by the presence of anterior radial sculpture. This assemblage of poorly known genera constitutes the Erviliinae (KEEN, 1969), a group with little taxonomic commendation. ROOIJ-SCHUILING (1972, 1973) ranked both *Spondervilia* and *Rocheffortina* as junior subjective synonyms of *Ervilia*, leaving only *Argyrodonax*, *Coecella*, and *Ervilia* as members of the Erviliinae.

FRENKIEL (1979) has argued that the presence of a